Research Focus

The importance in fishery management of leaving the big ones

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Research by Berkeley et al. and by Bobko and Berkeley has recently demonstrated that older individuals of some fish species produce larvae that have substantially better survival potential than do larvae from younger fishes. These new findings augment established knowledge that larger individuals usually have exponentially greater fecundity. This is important because commercial fisheries and especially recreational fishing often target the larger fish. The protection of larger or older individuals is necessary for the sustainability of species currently exploited by humans.

Not all larvae are of equal quality

Fisheries science models have been based on assumptions that the eggs and larvae from all fish within a population are of equal quality. Recent research [1–3] has shown that this fundamental assumption can be false. Larvae produced by older female black rockfish *Sebastes melanops* grow more than three times as fast and survive starvation more than twice as long as do larvae produced by younger females [1]. Furthermore, older fishes can be more experienced and successful at spawning, can provide the population with a longer spawning season and, as larger fishes, have an exponentially greater fecundity [1–3]. Selective harvesting of older individuals leads to the exponential reduction in the number of larvae produced, a shortening of the reproductive season, a decrease in the chance that some larvae of the population will encounter favorable conditions, a lowering of the average survival potential of larvae produced, selection for slower growth and reproduction at a smaller size [4] and, in extreme cases, lowering of genetic heterogeneity [5]. The selective removal of older or larger individuals probably contributes significantly to the impact of recreational fisheries [6,7] and to the difficulty that some populations experience in recovering from overfishing [8,9].

Public perceptions

Some sportsmen often believe that, by selectively harvesting the largest fish and leaving the rest, they cause less damage than does the commercial harvest of greater numbers and biomass. By leaving the juveniles to grow, they feel that they are reducing the dominance of the resources by a few older individuals, thereby enhancing growth of the smaller fishes, turnover and net yield.

However, based on the recent papers by Berkeley et al. [1,3] and by Bobko and Berkeley [2], sportsmen are, in fact, more likely to be selecting for slow growth and low yield by targeting the larger fishes [4]. Thus, to improve the growth rate of the fish and yield of the stock, they should instead target smaller fishes [4].

Recreational fishers also tend to believe that they are taking only a small portion of the fish stocks because, as individuals, they are taking fewer fishes than are individual commercial fishermen. However, with an expanding human population and improved technology, the intensity of recreational exploitation of coastal marine resources has increased substantially. For example, in an annual two-day event in Florida alone, ~50 000 sport fishers use scuba or snorkeling gear to reduce the population density of lobsters by 79–95% [10]. Until a couple of decades ago, the rate of fish capture was density dependent; that is, a smaller proportion of the total fish population was caught per unit time once the more-accessible fish had been caught and the fish population decreased in size. The remaining fish had a refuge in scarcity when fishers reduced their effort because the fish were rare and locating them took too much time. Modern technology and the increase in the human population have since reduced the effectiveness of the refuge in scarcity and the rate of take by recreational fishing is now becoming density independent.

A general pattern?

Berkeley et al. [1,3] and Bobko and Berkeley [2] suggest that the higher vitality of larvae produced by older adults is due to older fishes having more metabolic reserves [1–3]; thus, they are able to invest more energy in each offspring. In *S. melanops*, older individuals produce larger larvae, each provided with an oil droplet comprised primarily of energy-rich lipids that provide sustenance to the larva after the yolk sac is used up. By producing faster growing starvation-resistant larvae in greater numbers and over a broader time interval, the older fishes in a population provide a mechanism for reproductive bet-hedging for the variation in timing and abundance of zooplankton, the food supply for the larvae. Berkeley et al. [1] reviewed reports of other fish taxa and found examples of increased quality of progeny with maternal age (e.g. in haddock *Melanogrammus aegelfinus* and Atlantic cod *Gadus morhua*) and a five–tenfold increase in larval survival with increased larval growth rate (in bluefish *Pomatomus saltatrix* and Atlantic cod). Experimental

studies have shown that some invertebrates also share these traits. For example, larvae from larger bryozoan colonies can have 300% greater survival potential than can larvae from smaller colonies [11].

These initial studies by Berkeley *et al.* [1,3] and Bobko and Berkeley [2] and the publications that they cite indicate that the importance of older or larger individuals in fish and invertebrate populations might be crucial for the maintenance of resource stocks. The preliminary conclusions should be tested over a wide range of fish and invertebrate species. However, larval quality is unlikely to increase with age for all species of fish. It might be that there are no such differences in vitality of larvae from adults of different ages or sizes of short-lived fish or invertebrate species that reproduce only twice or a few times in their lives, or in pelagic species with more rapid population turnover (e.g. skipjack tuna *Katsuwonus pelamis* and mahimahi *Coryphaena hippurus*). It might be that it is only longer lived species that are most vulnerable to fishing pressure selective on the larger and older individuals.

Additional benefits of the larger ones

Even after successful recruitment, the larger individuals in a population can enhance the survival and reproductive success of the next generation. In some fishes, especially groupers, the young learn the route to spawning aggregations by following the more-experienced adults. Thus, as individual fishes of many species travel long distances to spawn in large aggregations, the selective removal of the larger adults could disrupt the reproductive process of the population as a whole.

Harvesting the larger individuals can also have ecological effects. By selectively removing the apex predators and higher trophic levels, entire food webs are reduced, changing the structure of the fish community and causing cascading ecosystem effects [12]. Even at lower trophic levels, the removal of larger herbivorous species and individuals within a species can also have large-scale effects on the benthic coastal ecosystems. For example, the biomass of parrotfishes each <20 cm in length has a different effect on the benthos than does the same biomass of parrotfishes each >20 cm length, because the smaller individuals do not excavate the substratum [13]. For example, in Bonaire, Netherlands Antilles, the larger parrotfishes can remove 7 kg m^{-2} y^{-1} from the shallow reef network, whereas the erosion by smaller parrotfishes is negligible [13].

Selective fishing pressure on the larger (older) individuals of fishes over recent decades has caused the rapid evolution of decreased body size and fecundity of some harvested fishes [14]. An evolutionary change more insidious than the reduction in body size and fecundity is the reduction of genetic heterogeneity. Hauser *et al.* [5] used microsatellite analyses to document a significant decline in genetic diversity of a New Zealand snapper *Pagrus auratus* population during the overharvesting of larger individuals. By using this example, Hauser *et al.* [5] demonstrated how marine fish stocks are vulnerable to the loss of genetic variability, potentially leading to reduced adaptability, population productivity and

persistence when the older members of the fish population are removed. The public and recreational fishers might see many medium-sized fishes in the population and perceive that the fish population is doing well and that there is no cause for concern. Hauser *et al.* [5] showed that the effective population size that determines the genetic properties of the population can be orders of magnitude smaller than the census population size perceived by the public and by the recreational and commercial fishers. This is especially true of sequential hermaphrodites.

Older fishes are usually also larger, and fecundity also increases exponentially with size. On average, a six-year-old *S. melanops* lays 374 fertilized eggs g^{-1} whereas a 16-year-old lays 549 eggs g^{-1} [2]. Thus, the reproductive potential of populations is disproportionately affected when fishermen target large individuals. This is especially true of sequential hermaphrodites, where all the larger individuals might be of a single sex; thus, any reduction in their number would severely limit the reproductive potential of the population.

What should we be doing?

We need to focus on protecting the larger or older individuals of long-lived fish species rather than concentrating on regulating the total numbers harvested from the population. Hawaiians traditionally used slot limits for more vulnerable species; for example, harvesting intermediate-sized moi *Polydactylus sexfilis* adults rather than taking the juveniles or large females. They apparently had an understanding of the importance of large females in the breeding stock. Present-day spearfishermen could also be encouraged to take intermediate-sized fishes. However, some fishing equipment, such as nets and hook-and-line, do not enable selection before taking, and fishes are harmed, often fatally,as a result of the use of catch-and-release methods. Berkeley *et al.* [3] conclude that the preservation of old-growth age structure in long-lived fishes can only be achieved by the establishment of networks of marine reserves.

Johannes pointed out that data-less resource management was the most effective approach to the complex and unpredictable interactions of resource management [15]. The information that is necessary to evaluate potential replenishment of marine resources relies not on statistical analyses of surveys of the population densities of stock or assessments of the catch-per-unit effort, but on the straightforward observation of whether the big ones are still there.

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Hybridization, transgressive segregation, genetic covariation, and adaptive radiation

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Analysis of adaptive radiation has had a central role in the development of evolutionary theory, but it is not clear why some groups radiate and others do not. Two recent papers by Albertson and colleagues on the genetic architecture of East African cichlid fishes implicate hybridization, transgressive segregation and genetic covariation in the early stages of adaptive radiation. Transgressive segregation and genetic covariation might be key innovations in genetic architecture that favor adaptive radiation.

Hybridization between members of conspecific populations and closely related species is common and has important evolutionary consequences [1]. One possible consequence is transgressive segregation (Box 1), which produces hybrid phenotypes that exceed the phenotypic range of the parental species and which might be a common phenomenon [2]. Transgressive hybrids can be sufficiently divergent from both parental species to establish a new hybrid species that can coexist with both parental forms. The potential for hybrids to found new species is enhanced if functionally related traits do not segregate independently, conserving associations (i.e. morphological integration; see [3]) among those traits in hybrid progeny. Seehausen [1] proposed that, when sympatric or parapatric species are genetically similar and readily hybridize, transgressive segregation can be instrumental in the origin of species. Now, Albertson and colleagues present evidence that transgressive

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segregation and genetic covariation of functionally related traits could have contributed to the explosive adaptive radiation of East African cichlid fishes [4,5].

Occurrence and causes of transgressive segregation

Rieseberg *et al*. [2] surveyed crosses between populations, inbred lines and closely related species of diverse animals, including a liver fluke, crustaceans, insects, teleost fishes, salamanders, frogs, lizards, birds and mammals, and several species of monocot and dicot angiosperms. Ninety-one percent of these studies reported at least one transgressive trait, and 44% of all traits were transgressive. Transgressive segregation appeared to be associated with inbreeding and to be more common in plants than in animals, although, for plants, this might reflect inbreeding. Diverse traits exhibit transgressive segregation, and they could contribute to ecological divergence and reproductive isolation between hybrids and parental species.

Rieseberg *et al*. [2] considered several possible genetic causes for transgressive segregation in hybrids. Apart from complementation among loci (Box 1), other possible causes are mechanistically implausible or can only account for a small fraction of cases. Their compilation indicated that transgressive segregation results from interactions among loci with alleles that have opposing effects on phenotypes within each parental species but could have reinforcing effects (i.e. complementation) in hybrid generations after the F1 generation. Albertson and colleagues [4,5] investigated the genetic basis for the evolutionary diversification of feeding (trophic) structures